# Cyclic evolution of phytoplankton forced by changes in tropical seasonality

https://doi.org/10.1038/s41586-021-04195-7

Received: 30 October 2020

Accepted: 29 October 2021

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Although the role of Earth's orbital variations in driving global climate cycles has long been recognized, their effect on evolution is hitherto unknown. The fossil remains of coccolithophores, a key calcifying phytoplankton group, enable a detailed assessment of the effect of cyclic orbital-scale climate changes on evolution because of their abundance in marine sediments and the preservation of their morphological adaptation to the changing environment<sup>1,2</sup>. Evolutionary genetic analyses have linked broad changes in Pleistocene fossil coccolith morphology to species radiation events<sup>3</sup>. Here, using high-resolution coccolith data, we show that during the last 2.8 million years the morphological evolution of coccolithophores was forced by Earth's orbital eccentricity with rhythms of around 100,000 years and 405,000 years-a distinct spectral signature to that of coeval global climate cycles<sup>4</sup>. Simulations with an Earth System Model<sup>5</sup> coupled with an ocean biogeochemical model<sup>6</sup> show a strong eccentricity modulation of the seasonal cycle, which we suggest directly affects the diversity of ecological niches that occur over the annual cycle in the tropical ocean. Reduced (or enhanced) seasonality in surface ocean conditions favours species with mid-size (large and small) coccoliths, increasing (or decreasing) coccolith carbonate export and burial. We posit that eccentricity pacing of phytoplankton evolution contributed to the strong 405,000-year cyclicity that is seen in global carbon cycle records.

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Coccolithophores precipitate half of the biogenic CaCO<sub>3</sub> that is exported from the open ocean<sup>7</sup> and their fossil platelets (coccoliths) first appeared in sediments during the Upper Triassic, around 215 million years ago (Ma). Thereafter, coccolithophores rose to dominance<sup>8</sup> and became a key biological modulator of the global carbon cycle through photosynthesis and calcification<sup>9</sup>. In the dominant Cenozoic Noelaerhabdaceae family (including Emiliania huxleyi and Gephyrocapsa), species are defined by the morphological characteristics of their coccoliths, with size being a key criterion<sup>10</sup> that is related to cell size<sup>11</sup>. For *Gephyrocapsa* and *Emiliania*, phylogenies reconstructed from gene sequences indicate that morphology-based definitions correspond to biological species<sup>3,12</sup>. Within a given Noelaerhabdaceae population-which is typically dominated by one species but includes several-interspecific and intraspecific changes in coccolith length and mass occur in response to environmental parameters such as carbonate chemistry<sup>1</sup> and temperature<sup>2</sup>. Studies of coccolithophore evolution have focused on geological-timescale changes in species richness and turnover<sup>13</sup>, coccolith carbonate accumulation<sup>8,14</sup> or calcification potentially driven by carbon cycle changes<sup>15</sup>. In addition, climate changes induced by orbital cycles (on timescales of tens to hundreds of thousands of years) strongly influence the composition of nannofossil assemblages<sup>16-18</sup>. However, so far the effects of orbital cycles

on coccolithophore evolution, coccolith morphology and carbonate production have not to our knowledge been examined simultaneously.

Here we quantify the Pleistocene history of tropical Noelaerhabdaceae evolution at high resolution (around two thousand years, kyr), using coccoliths preserved in nine well-dated sedimentary sections from the Indian and Pacific Oceans cored during International Ocean Discovery Program (IODP) and International Marine Past Global Changes Study (IMAGES) expeditions (Extended Data Table 1). We use artificial intelligence microscopy to create a biometric database of over 7 million coccoliths from more than 8,000 samples (Methods). The strong similarity of morphometric patterns observed at each site (Extended Data Fig. 1) led us to build composite frequency contour plots of coccolith size and mass, representing larger-scale evolutionary change (Fig. 1a, Methods). Patches denoting high frequency of a particular size correspond in many cases to described acmes of Noelaerhabdaceae species<sup>19-21</sup> or proposed evolutionary events<sup>3</sup> (Fig. 1). The most recent evolutive phase, which started around 550 thousand years ago (ka), is attributed to a radiation event and the emergence of new Gephyrocapsa species, on the basis of a genetic study of extant taxa and its temporal correlation to low-resolution coccolith morphometric data<sup>3</sup>. Over the Pleistocene, average coccolith size shows an increase that corresponds to a gradual shift in dominance from smaller

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Q13

to larger coccoliths (Fig. 1b). On orbital timescales, global ice volume and deep-sea temperature as represented by benthic foraminiferal  $\delta^{18}$ O show a dominance of 41-kyr and later around 100-kyr glacial–interglacial cycles<sup>22</sup> (Fig. 1c). By contrast, average coccolith length follows a regular cycle that is highly coherent (greater than 99.9%) with the orbital eccentricity periods of 405 kyr (e405) and of 124 and 95 kyr (e100)<sup>23</sup> (Extended Data Fig. 2a), with larger average size occurring at high eccentricity with a slight time lag (Fig. 1b).

Average size or mass of coccoliths in a Noelaerhabdaceae population may vary because of macro- and/or microevolution, or because ecological changes modulate the relative abundances of species in different size ranges. To build a metric that describes only species evolution, we remove the effect of relative abundance changes related to ecology<sup>24</sup> by formulating a morphological divergence index (MDI), calculated as the difference in average coccolith mass between two size classes-larger and smaller than 3 µm (Methods). Thus, MDI quantifies morphological divergences of species over time through evolution, and could be driven by changes in size or degree of calcification (see Fig. 2 for a conceptual explanation). Noelaerhabdaceae coccolithophores spread rapidly throughout the oceans and are often cosmopolitan, resulting in the same species being present in many regions, but with different relative abundances<sup>12,19</sup>. MDI varies independently of regional ecological specificities, and MDI records from sites in distinct oceanographic biomes<sup>25</sup> and climatic regimes (for example, warm pool, monsoon-dominated; Extended Data Table 1) are highly intercorrelated, all showing significant e405 and e100 periods (Extended Data Figs. 1, 2). Therefore, we produce a composite MDI stack, which preserves the high resolution of each dataset (Fig. 1e, Methods). The MDI stack, interpreted as reflecting evolutionary changes in morphological diversity, shows strong 405-kyr pacing throughout the Pleistocene irrespective of glacial-interglacial background state. Cross-spectral analysis indicates significant (greater than 90%) coherency between the stack and Earth's eccentricity periods since 2.8 Ma (Fig. 1d). This pattern cannot be the result of differential dissolution on coccolith morphology (see Methods) and in contrast to MDI, Pleistocene deep-sea CaCO<sub>3</sub> dissolution generally follows glacial-interglacial cycles<sup>26</sup>. Similarly, coccolith morphological evolution appears not to be responding directly to physical parameters covarying with global ice volume, such as sea level or ocean temperature. Although eccentricity forcing on coccolithophore productivity has previously been suggested<sup>27,28</sup>, our new dataset reveals that eccentricity cycles instead forced the evolution of the Noelaerhabdaceae.

Cyclic coccolithophore evolution may have affected the ocean carbon cycle through coccolith carbonate production and burial in sediments<sup>14,29</sup>. Coccolithophores produce large amounts of calcite during blooms<sup>27,30</sup>, and sediments are often dominated by a few opportunistic species, for example E. huxleyi (0-90 ka)19 and Gephyrocapsa caribbeanica (280-570 ka)<sup>20</sup> in the late Pleistocene. We estimate the mass accumulation rate of Noelaerhabdaceae coccoliths (NoMAR) in our cores and produce a stacked record (Fig. 1g, Methods). Noelaerhabdaceae coccoliths represent on average half of the total calcareous nannoplankton mass in our studied cores (Extended Data Table 2). The two components of NoMAR, coccolith flux and average mass, are separated in Extended Data Fig. 3. This reveals that NoMAR is primarily driven by changes in coccolith flux, and that flux and mass often have opposing effects on NoMAR as medium-sized, lighter species (for example, E. huxleyi and G. caribbeanica) contribute the most to coccolith carbonate export. Thus, higher NoMARs when mid-size opportunistic species dominate often correspond to lower MDI values (Fig. 1e, g). The dominance of these opportunistic species coupled with high coccolithophore accumulation in sediments during eccentricity minima is also recorded in the extra-tropics<sup>27</sup>. In contrast to MDI, local ecological conditions affecting productivity and export-and possibly water depth affecting coccolith accumulation-also influence NoMAR, so a linear relationship between the two is not expected. Although it is impossible to quantify the relative effects of these factors, common trends between sites emerge despite different absolute values and these are reflected in the NoMAR stack. Thus, NoMAR combines global evolutionary and local ecological drivers of calcite production, whereas MDI should exclusively record evolution. Nevertheless, the NoMAR composite record shows strong eccentricity periodicities that are significantly coherent with MDI throughout the Pleistocene (Fig. 1f), showing a strong imprint of coccolithophore morphological evolution on carbonate production and burial.

#### MDI and long-term seasonal variations

We hypothesize that the MDI index responds to variations in the amplitude of tropical seasonality. In low latitudes, seasonal contrast is related to the eccentricity of Earth's orbit<sup>23,31</sup> both directly, because the ellipticity of the orbit determines the distance between the Sun and the Earth during each season, affecting radiation intensity, and indirectly, because eccentricity modulates the effect of precession on seasonal insolation contrast. Seasonal contrast is greater during periods of high eccentricity. To our knowledge, the eccentricity-paced rhythm of surface-ocean seasonality that dominates MDI has not been documented previously because most proxies record integrated annual average conditions or a specific season. In the modern intertropical ocean, large seasonal changes in the properties of the upper water column (for example, mixed-layer depth and nutrient availability) are associated with the seasonally reversing monsoon systems and latitudinal migrations in the intertropical convergence zone. The seasonal succession of coccolithophore species, a characteristic of phytoplankton ecology, is indicative of their adaptation to the different ecological niches created by seasons<sup>24</sup>. In the modern ocean, the highest phytoplankton diversity is found in the tropical band, a pattern probably related to high temperatures and stable conditions, whereas seasonal species turnover is highest at mid-latitudes because of a strong seasonal temperature contrast<sup>32</sup>. Intra-annual dynamics of net primary production (NPP) are good descriptors of the range of oceanographic niches and biomes<sup>25</sup>, because NPP represents the integrated biological response to all of the changes forced by the ocean-atmosphere coupled system. To demonstrate the effect of orbital configuration on NPP seasonality and therefore niche availability, we simulated monthly oceanic NPP using the fully coupled IPSL-CM5A2 model<sup>5</sup>, which includes the ocean biogeochemistry model PISCES-v26, for seven early Pleistocene time intervals that cover a large eccentricity spectrum with different precession conditions but with similar ice volume and obliquity (Extended Data Table 3, Fig. 1b). The results of these simulations for the tropical Indian and western Pacific Oceans show that the seasonal range of NPP increases with eccentricity, a trend that parallels the eccentricity sorted values of MDI in our Plio-Pleistocene time series (Fig. 3).

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In the simulations, the increase in amplitude of the NPP seasonal cycle (Fig. 3a, Extended Data Fig. 4a–e) is primarily driven by higher productivity during boreal summer, especially in the eastern Indian ocean. This increase is forced by the modification of atmosphere-ocean dynamics in response to variations in the amplitude and seasonality of insolation forcing (Extended Data Fig. 5a-c). Eccentricity acts on sea-level pressure over continental Asia (Extended Data Fig. 5d-h) through insolation, inducing modifications of sea-level pressure gradients and low-level wind circulation over the Indo-Pacific Warm Pool (IPWP) (Extended Data Fig. 4f-h). Changes in atmospheric dynamics are responsible for regional and seasonal enhancement of NPP at high eccentricity (Extended Data Fig. 4a-c), either through the generation of anomalous upwelling along the equator (southwest of India) or the modification of the hydrological cycle that create more favourable conditions for intense vertical mixing (Extended Data Fig. 6a, c), depending on precession. Overall, those localized increases in the amplitude of the seasonal cycle lead to a less homogeneous upper ocean in the IPWP region at high eccentricity (Fig. 3a, Extended Data Fig. 4a-c). We propose that during times of high eccentricity, the higher seasonal



 $\label{eq:Fig.1} Fig.\,1 | No elaerhabdace a ecoccolith morphology and accumulation,$ 

eccentricity, and climate over the last 2.8 million years. a, Frequency contour plot of multi-site stacked coccolith length (see Methods). Scanning electron microscope images represent examples of the diversity of Noelaerhabdaceae morphologies over time. 1, *Emiliania huxleyi*; 2, *Gephyrocapsa ericsonii*; 3, *Gephyrocapsa oceanica*; 4, *Gephyrocapsa caribbeanica*; 5–6, *Gephyrocapsa omega*; 7–8, mid-size *Gephyrocapsa*; 9, small *Gephyrocapsa*; 10, *Pseudemiliania ovata*; 11, *Reticulofenestra minuta*; 12, left: *P. ovata*, right: *R. minutula*. **b**, Mean coccolith length in the stack (blue), plotted with Earth's eccentricity<sup>23</sup> (dotted black line) and low-pass-filtered eccentricity with an angular frequency of 0.021 kyr<sup>-1</sup> (red). Described Noelaerhabdaceae acmes<sup>19-21</sup> are shown as black bars (I, *E. huxleyi*; II, *G. caribbeanica*; III and IV, mid-size *Gephyrocapsa*). Coloured stars and diamonds on the eccentricity curve show the timing of actual orbital configurations used in model simulations  $(P_{max}, perihelion in December; P_{min}, perihelion in June); smaller grey symbols indicate times throughout the record with similar eccentricity and precession configurations to those modelled (Methods).$ **c** $, LR04 benthic foraminiferal <math>\delta^{18}$ O stack<sup>22</sup>. Grey band illustrates the small range of benthic  $\delta^{18}$ O between model simulations. **d**, Left, evolutive cross-spectral analysis between MDI and eccentricity (Methods). Colour-scale shows coherency (90% confidence level (CL) above 0.7); horizontal dashed lines show eccentricity periods. Right, MTM spectral analysis of detrended MDI stack. Shaded areas are above the CL90% (dashed line). Solid black line is CL95%. **e**, MDI stack (2-kyr resolution; see Methods). **f**, Left, evolutive cross-spectral analysis of detrended NOMAR and MDI. CLs as in **d** (left). Right, MTM spectral analysis of detrended NoMAR stack. CLs as in **d** (right), **g**, NoMAR stack (2-kyr resolution; see Methods). MDI and NoMAR stacks are smoothed with a Loess function, and blue shading shows maximum and minimum values across all records.

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**Fig. 2** | **MDI concept. a**, Schematic representation of MDI (conceptual model). We consider an evolutionary sequence in which species A (intermediate morphology) evolves into species B (smaller) and C (larger). In epoch 2, B and C have equivalent proportions, and in epoch 3, they fluctuate in relative abundance between 25% and 75%. The evolutionary event between epochs 1 and 2 (red shading) is not detected in mean population morphology (for example, size, mass). In epoch 3, fluctuating ecology produces population dynamics detected in mean morphology (grey shading). With a biometric boundary of 2 units, MDI jumps from 0 to 2 from epoch 1 to 2, thus it is diagnostic of an evolutionary event. In epoch 3, MDI remains stable despite fluctuating assemblage composition. In this idealized example, average population biometry is related to ecology and MDI to evolution. **b**, MDI calculated for IODP site U1485 (example dataset). Right, average Noelaerhabdaceae coccolith mass (smoothed using a Loess function). Middle,

range of NPP in our model simulations (representing up to 100% of mean annual NPP) is indicative of more diverse ecological niches to which coccolithophores can adapt. A greater diversity of ecological niches when seasonality is high<sup>25</sup> leads to a larger number of species because Noelaerhabdaceae adaptation is characterized by the adjustment of coccolith size and degree of calcification to thrive in the new environments<sup>1,2</sup>.

## Eccentricity lag, origination and dominance

Coccolith morphological diversity clearly responds to eccentricity (Fig. 1); however, in stark contrast to Plio-Pleistocene climate proxy records<sup>22,33</sup> and coccolithophore assemblage dynamics<sup>16-18</sup>, precession and obliquity cycles are absent from the 2-kyr resolution MDI records (Extended Data Fig. 2c-k). These cycles could have been smoothed out by the evolutionary process acting as a low-pass filter, providing an explanation for the phase lag observed between eccentricity and Noelaerhabdaceae morphology (Fig. 1b, Extended Data Fig. 2a, b). We know that speciation events spread rapidly throughout the oceans<sup>12,19,21</sup>, and species dominance takes longer, as exemplified by E. huxleyi. This species appeared at 290 ka but did not become dominant until 90 ka<sup>19</sup>, during an intense low-eccentricity interval two e100 cycles later, when it gained a competitive advantage over Gephyrocapsa oceanica and Gephyrocapsa ericsonii (Extended Data Fig. 7). The delay between species appearance and dominance could therefore be intrinsic in smoothing out variability at precession and obliquity timescales in the MDI record (Fig. 1b, Extended Data Fig. 7). At present, the lack of precise ages for the first occurrences of Noelaerhabdaceae species in the fossil record precludes us from testing this hypothesis further.

two size classes are created: coccoliths shorter and longer than 3 µm (grey histograms). MDI is the difference between the average log(mass) of each class (light and dark grey dots on histograms). Thus, MDI can differ substantially from average coccolith mass (black dots on mass distribution plots), and two samples can have a similar MDI but different average mass and mass distributions (for example, 180 ka versus 190 ka), or different MDI but similar averages (for example, 3 ka versus 190 ka). In this way, MDI isolates morphological variability resulting from evolutionary changes in the number of different morphotypes present within the population. Left, MDI record (identical Loess smoothing window to that in the right panel). Smoothed curves illustrate the effect of different length or mass thresholds used to calculate MDI: solid red line, 3 µm; red dotted line, 2.7 µm; red dashed line, 3.6 µm; solid blue line, 3.16 pg.

The eccentricity lags and transfer of spectral power from high to low frequencies described here are analogous to modelling results in a previous study of deep-time carbon cycle variations on orbital time-scales<sup>34</sup>, hinting that coccolithophores may drive-rather than just respond to-carbon cycle changes.

## Coccolithophores and the global carbon cycle

The persistence of e100 and e405 cycles in Cenozoic and Mesozoic records of the ocean carbon cycle (for example, per cent CaCO<sub>3</sub> and for a miniferal  $\delta^{13}$ C), independent of glacial-interglacial climate state, attests to the importance of biogeochemical processes operating at these timescales throughout Earth's history<sup>35,36</sup>. During the Pleistocene, Mediterranean surface  $\delta^{13}$ C records document e405 cycles more faithfully than do deep open-ocean records, suggesting a low-latitude climatic origin of this signal<sup>28</sup>. Chemical weathering has been suggested as a potential modulator of the ocean carbon cycle on 400-kyr timescales<sup>37</sup>. Similar to our coccolith records, a notable phase lag between  $\delta^{13}$ C and eccentricity is observed in the e405 band, which has been explained by the long residence time of carbon in the oceans and resultant transfer of energy from precession into eccentricity bands through a non-linear process<sup>34,35</sup>.Previous coccolith records spanning up to Q19 around 1 million years (Myr) have linked coccolithophore production to eccentricity forcing<sup>17,27</sup>. Yet changes reconstructed at our low-latitude sites cannot be explained by the hypothesis that eccentricity-driven changes in growing season length are responsible for the approximately 400-kyr cycle in coccolithophore production<sup>27</sup>. Our data and model results support the alternative hypothesis that changes in seasonality caused by the eccentricity of the Earth's orbit paced tropical



### $Fig.\,3\,|\,Modelled\,NPP\,seasonal\,contrast\,under\,different\,eccentricity$

configurations and MDI. a, Eccentricity-driven changes in the seasonality of NPP in the tropical Indo-Pacific. Colour scale shows the vertically integrated NPP seasonal contrast difference between numerical model outputs computed at maximum and minimum eccentricity, each run at perihelion in June  $(P_{min})$  and December  $(P_{\text{max}})$  and then averaged (Methods) (that is, Seasonality  $E_{\text{max}}$ Seasonality  $E_{\min}$ ). Values are expressed as a percentage of mean annual pre-industrial NPP simulated in a previous report<sup>5</sup>. Red colours imply higher seasonality at high eccentricity; blue colours imply higher seasonality at low eccentricity. Black circles show sediment core site locations used in this study: 1, IODP U1446; 2, IODP U1448; 3, IODP U1443; 4, MD97-2140; 5, MD05-2920; 6, IODP U1486; 7, IODP U1485; 8, MD05-2930; 9, IODP U1483 (Extended Data Table 1). Exact core locations are not relevant, as recorded evolutionary events may have originated anywhere in the tropics. **b**. Box-and-whiskers plots of all MDI values (centre line, median; box limits, first and third quartiles; whiskers, 1.5× inner quartile range; points, outliers), sorted by increasing low-pass-filtered eccentricity and grouped into four bins (e < 0.01 (number of samples, n = 179); 0.015 < e < 0.025 (n = 328); 0.025 < e < 0.035 (n = 513); and e > 0.035 (n = 386)), compared to the seasonal NPP contrast (maximum minus minimum month) from seven numerical simulations (see Methods). Model points represent a regional mean of the entire map area in a. As in Fig. 1b, orange diamonds are model runs with perihelion in December ( $P_{max}$ : 2,222 ka, 2,265 ka and 2380 ka), green stars are runs with perihelion in June ( $P_{min}$ : 2,230 ka, 2,346 ka, 2,369 ka, and 2,395 ka)-illustrating that eccentricity has a much larger effect on seasonality than precession at a given eccentricity.

Noelaerhabdaceae evolution and production throughout the Pleistocene. Although these changes clearly affect carbonate accumulation patterns (Fig. 1g), coccolithophore productivity alone cannot be responsible for the expression of long eccentricity cycles in climate records because they are only one constituent of the phytoplankton. Other phytoplankton groups, some with little or no fossil record, may also have been similarly influenced by variations in tropical seasonality on these timescales. In this case, the effect of changes in the ratio of exported organic carbon production to carbonate mineral production, known as the rain ratio<sup>38</sup>, may have been strong enough to modulate the carbon cycle. The cyclic evolution of calcifying phytoplankton on eccentricity timescales in response to seasonality documented here provides evidence in support of the hypothesis that biosphere productivity must have responded to changes in solar insolation<sup>35,37</sup> to explain the strong e405 signature in carbon cycle records.

#### **Online content**

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Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-021-04195-7.

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